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Deciphering the black spruce response to climate variation across eastern Canada using a meta-analysis approach

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A R T I C L E I N F O

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A B S T R A C T

Boreal forests are experiencing climate change more rapidly than other biomes, which is likely to impact their future management. Understanding how tree growth responds to regional and seasonal variation in climate is essential to anticipate future management of boreal forests. We compiled and summarized black spruce climate-growth relationships from 11 dendroclimatology studies in boreal forests of Northeastern North America. Using a statistical synthesis of 113 sites and 2,995 black spruce trees, latitudinal trends were found to affect the growth response to monthly climate variables. Below 50°N, a high portion of sites showed a negative growth response to summer temperatures, whereas these were positive between 50°N and 54°N. Growth response to previous summer precipitation was consistently positive across latitudinal range. This shift from negative to positive growth response to summer temperatures observed between 50 and 51°N was confirmed through meta-analysis and was found to be associated with a mean annual temperature of ~ 0 °C. This threshold is likely representative of the limit at which black spruce growth shifts from being moisture- to temperature-limited. By directly relating growth-climate relationships to mean annual temperature and precipitation at a given site, our meta-analysis allows readers to easily grasp the current growth response of black spruce to climate variation. Combined with climate projections, our results may also be used to facilitate the estimation of black spruce growth trends through time, and thus inform the implementation of adaptative silvicultural measures.

1. Introduction

Boreal forests cover 27% of the Earth's forested areas (FAO, 2020) and are experiencing climate change at a rapid rate that will likely impact the way they are managed and harvested in the future (IPCC, 2014). Across the boreal forest of North America, climate models currently project increases in mean annual temperature and heterogenous changes to precipitation regimes (Price et al., 2013; Wang et al., 2014). Warmer spring temperatures and earlier snowmelt are also likely to contribute to a longer growing season (Linderholm, 2006). Such changes are likely to influence tree growth and species distribution, with productivity expected to increase where annual temperature limits growth and the opposite in regions experiencing moisture stress (McKenney et al., 2007, D'Orangeville et al., 2016). Beyond the uncertainty of future climate scenarios and associated model projections (Mahony et al., 2021), the spatial heterogeneity of the growth response to climate variation also limits the predictability of future boreal forest productivity. In turn, such uncertainty complexifies the design and implementation of adaptive silvicultural practices (Achim et al., 2021). Climate-growth relationships, which can be explored using dendrochronology, are commonly used to investigate variation in intra- and inter-species tree growth (usually as a measure of annual radial growth) in response to regional and seasonal variation in climatic variables. Exploring such historical relationships can help forest managers better understand variation in the climatic drivers of tree growth across temporal trends (Babst et al., 2019) to potentially predict future forest growth under a changing climate.

Within boreal forests, black spruce (*Picea mariana* (L.) Mill B.S.P.) represents the most abundant tree species in Canada and provides over 35% of merchantable wood volume for both Ontario and Québec provinces (MFFP, 2018; OMNRF, 2021). Yet, climate-growth research has generally been region-specific and has generated contradicting results (Nicault et al., 2015; D'Orangeville et al., 2016). Most commonly, black spruce interannual radial growth has been found to respond

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negatively to previous summer temperatures (Huang et al., 2010, Ols et al., 2018, Marchand et al., 2019) and low precipitation (D'Orangeville et al., 2016, Marchand et al., 2019), particularly in southern regions where black spruce growth is moisture-limited (Sniderhan et al., 2021). In contrast, growth has been reported to respond positively to previous summer precipitation, current winter and spring temperatures (Huang et al., 2010, Marchand et al., 2019) and longer growing seasons, particularly in regions characterized by relatively cool annual temperatures where growth is often temperature-limited (Girard et al., 2011). Among the few broader-scoped studies, D'Orangeville et al. (2016) linked water availability and air temperature to interannual growth of>26,000 black spruce trees from 16,450 stands across 583,000 km^2 in eastern Canada (Québec). Their results showed that at northern latitudes (>49°N), warmer temperatures had a positive effect on radial growth even in conditions of low water availability. At more southern latitudes (<48°N), black spruce growth was positively correlated to increasing water availability (D'Orangeville et al., 2016). It can therefore be suggested that where low temperature restricts forest growth (north of 49°N), black spruce forests are likely to respond positively to future projections of warmer temperatures and reduced precipitation. A similar study by Marchand et al. (2019), quantified 1,914 black spruce trees over 812 sampling plots across Québec above 50°N and found that while black spruce growth was steadily declining between 1970 and 2005, it was negatively correlated to previous year summer temperature and current year spring precipitation. Conversely, growth was positively correlated to winter precipitation and winter temperature (Marchand et al., 2019). This suggests that potential growth increases from warmer than average early summer temperatures can be negated by the more frequent occurrence of intense heat waves even at latitudes north of 49°N.

Such results have important implications for region-specific forest management. Variations in black spruce climate-growth relationships may be particularly pronounced in eastern Canada as the region is characterized by a strong north–south temperature gradient and east–west precipitation gradient, allowing precipitation to compensate for greater evapotranspiration caused by warmer temperatures in the east (Gauthier et al., 2015). It is currently unclear whether such a shift from negative to positive growth response with increasing latitude will continue throughout the century (D'Orangeville et al., 2018), or occur in the more central and western parts of the biome. Similarly, results from other studies conducted outside limits of harvestable black spruce forests (Marchand et al., 2019) may not be applicable to more intensively managed forests in more southern regions. To date, broad-scale studies investigating black spruce climate-growth relationships in eastern Canada focused either on harvestable or non-harvestable forests and were restricted to provincial borders. In parallel, although multiple studies have investigated the growth response of black spruce to climate, extracting locally relevant assessments of current trends is difficult due to the high variability among results. An improved understanding of the current response to climatic variation will help better anticipate how productivity is likely to change in the upcoming century and forecast how silvicultural strategies should be adapted to economically meet demands in a changing climate.

In this study, we compiled black spruce climate-growth relationships from dendroclimatology studies at different locations in the boreal forests of eastern Canada using statistical synthesis and meta-analysis approaches. In doing so, we aimed to summarize climate-growth relationships at a vast spatial scale to better anticipate the impact of a changing climate on black spruce productivity in the eastern Canadian boreal forest. We first compiled results from previous studies to identify the most important climatic drivers of black spruce radial growth. Secondly, we investigated the effect of local climate variables on climate-growth relationships to produce location-specific predictions of the correlations between black spruce radial growth and monthly climate variables. Our results will provide meaningful and comprehensible inputs on the influence of local climate on growth-climate relationships that can be easily used to evaluate present and future growth trends for black spruce across eastern Canada.

2. Method

2.1. Selection of studies

Peer-reviewed publications evaluating climate-growth relationships for black spruce were gathered using Web of Science. The following strings of keywords were used as searching query: ("radial growth" OR growth OR dendro* OR tree-ring) AND (climat* OR dendroclimato*) AND ("eastern Canada" OR Québec OR Ontario OR Newfoundland) AND ("black spruce" OR "*Picea mariana*"). The search yielded a total of 320 results, from which relevance was first evaluated based on the title and abstract. Methods sections were also screened when necessary. We selected publications reporting results from eastern boreal Canada and using annual tree growth evaluated through tree-ring widths using high-quality cross-dated series (*i.e.,* supported by analyses in COFECHA (Holmes, 1983) or similar programs). To be considered, publications had to clearly state the number of sampled trees and precise site location. Reference lists from the selected publications were also screened to find additional studies that could be relevant. A total of 26 studies matched our criteria, with most studies focusing on the influence of monthly climatic variables (n = 18), which were retained for further analysis.

2.2. Statistical synthesis

To summarize the influence of monthly climatic variables on the radial growth of black spruce, we selected publications considering monthly mean temperature and/or total precipitation from previous summer to the end of the current summer. We retained publications evaluating the effect of these metrics through correlations or response functions, regardless of whether bootstrapping was performed. Such methods were common in the considered publications (n = 14), whereas the use of other types of analyses, such as pointer years (n = 1) or stepwise variable selection (n = 3), were scarcer. Results of three of the 14 publications could not be extracted, either because they were pooled (not presented for each site location), or data were analyzed using moving temporal windows. Ultimately, 11 publications were retained that presented results of dendroclimatic analysis investigating the effect of monthly mean temperature and/or total precipitation (Table 1). Most of these publications focused on Québec or Labrador (n = 10), whereas one took place in eastern Manitoba. Taken together, these publications provided climate-growth relationships for 113 sites, using a total of 2,995 black spruce trees. From these, the influence of monthly precipitation was investigated at 80 sites, whereas that of monthly mean temperature was investigated at 109 sites.

To summarize the influence of the monthly climatic variables, we extracted the direction of the significant effects ($\alpha = 0.05$) for the smallest sampling unit presented in each paper. Such sampling units were usually a site or a combination of sites (hereafter referred to as 'site'). Because some publications provided only p-values or effect directions and not values for correlation coefficients or response functions, we first used a method analogous to vote counting to summarize the results of the selected publications. This method does not consider the effect size, nor the sample size (Borenstein et al., 2007), which are important shortcomings from a statistical point of view. However, it was well suited to our objective in this first step of our analysis of identifying the most relevant monthly climatic variables that could be linked to the interannual variation of radial growth in black spruce.

We compiled the number of sites showing positive, negative, and non-significant relationships with monthly mean temperature and total precipitation from the previous to the current summer. We reported the proportion of sites showing positive and negative associations with each climate variable to estimate the general direction of the effect and its

Table 1
Description of studies from which black spruce growth response to monthly climate variable[a] were obtained. Latitude and longitude present the spatial extent of the sites investigated for each study. Period refers to the temporal extent of the dendrochronological series and corresponding climatic data."n" is the total number of trees included in each study."Var" indicates the climatic variables tested; mean monthly temperature (T), total monthly precipitation (P), or both (TP). "x" in the Meta column indicates that correlation coefficients with monthly variables were extracted and used in the meta-analysis.

Authors	Latitude	Longitude	Period	Sites	n	Var	Method	Meta
Huang et al., 2010	46-54°N	77-79°W	1950–2003	9	193	TP	Bootstrapped correlation coeffficient	
Ols et al., 2016	51-52°	68-77°W	1901–2001	3	895	TP	Correlation function + response function	x
Girardin et al., 2008	51.5°N	101°W	1912–1999	2	496	TP	Correlation coefficient	
Nishimura and Laroque 2011	51-55°N	61-66°W	1971–2008	7	140	T	Response function	
Fierravanti et al., 2015	48-51°N	70-73°W	1901–2011	4	77	P	Bootstrapped correlation coeffficient	x
Hofgaard et al., 1999	48-50°N	78-80°W	1914–1993	5	157	TP	Bootstrapped correlation coeffficient	x
Girard et al., 2011	47-53°N	70-72°W	1928-1998[b]	53	530	TP	Response function	
Trindade et al., 2011	53.6°N	58.8°W	1971–2000	1	30	TP	Correlation coefficient	
Dumeresq et al., 2010	51-55°N	57-60°W	1942–2006	9	188	T	Correlation function + response function	x
Mamet and Kershaw 2011	57-59°N	93-94°W	1901-2002[c]	3	111	TP	Correlation function + response function	x
Wang et al., 2020	51-56°N	60-74°W	1901–2000	17	178	T	Correlation coefficient	

[a] Monthly climate variables were included from previous June to current August in all studies except for Girardin et al., (2008) which was for previous July to current August.
[b] Maximum range; varies according to the weather station, latest start = 1968, earlier end = 1985.
[c] 1929-2002 for precipitation data.

consistency across sites. We also investigated spatial trends (mainly latitudinal) by mapping the effect direction for each site and each monthly variable. The proportion of sites responding negatively and positively to the monthly climate variables was also calculated for each two-degree-increment in the latitudinal range covered by the study sites. All maps and statistical analyses were computed in the R statistical programming software (R Core Team, 2019).

2.3. Effect of site conditions on growth-climate relationships

We used a meta-analysis approach to investigate the effect of site conditions on climate-growth responses. When available, we extracted correlation coefficients from publications between tree-ring widths and a) monthly temperature, and b) precipitation. When results were presented as figures, correlation coefficients were extracted using WebPlotDigitizer (version 4.0., Rohatgi 2018). Results presented as heatmaps were not included as correlation coefficients could not be extracted precisely. We also extracted sample sizes associated with each coefficient. Five of the eleven studies presented extractable correlation coefficients, representing a total of 24 sites (Table 1). Twenty sites reported correlation coefficients between growth and monthly temperatures, whereas 15 reported correlation coefficients between growth and monthly precipitation.

For each site location, mean annual temperature (MAT) and mean annual precipitation (MAP) were modelled for the 1971–2001 period, using BioSim (Version 11; Régnière et al., 2017). This period constitutes the most recent dataset available in BioSim as the software implements climatic normals on 30-year periods, and overlaps all dendrochronology analyses from the selected studies. MAT and MAP were modelled using the four nearest weather stations from each site and climate normals for the 1971–2001 period. Because MAT, MAP and latitude showed strong collinearity ($R > 0.7$), the influence of each predictor was tested in separate models. Mixed-effects meta-regressions were then implemented using raw monthly correlation coefficients as outcome measure and latitude, MAT, and MAP as predictors. A random effect was added for each study site (Viechtbauer, 2010) and *meta*-regressions were built independently for each monthly variable using the function "rma" of the "metafor" package (Viechtbauer, 2010). We used an unweighted meta-analysis approach as we were interested in isolating the effect of site-specific climate and location on growth responses. When attempting to use a formally weighted meta-analysis, our ability to isolate site-specific effects was limited by the variation in sample sizes across studies and the analysis became overly focused on a small subset of sites with larger sample sizes. Although less statistically powerful than a weighted meta-analysis, unweighted meta-analysis provides an appropriate estimate of the overall mean of effect sizes (Gurevitch and Hedges, 1999). Indeed, the overall mean of effect sizes is not biased by sampling error, in contrast with the effect magnitude (*i.e.* the mean absolute values; Nakagawa and Lagisz, 2016; Morissey, 2016).

For each model, heterogeneity was estimated using restricted maximum-likelihood estimator (REML; Viechtbauer 2015). Significance and confidence intervals of the effect of predictors were estimated using the Knapp and Hartung (2003) method. Outliers were carefully checked for each model using the function "influence" of the "metafor" package. Accordingly, three sites (from Mamet and Kershaw, 2011) were removed from the dataset when investigating the impact of MAP on radial growth, as MAP strongly differed from other locations in these sites (~50% of that recorded elsewhere). Publication bias was also verified using funnel plots with the standard error as the y-axis and regression test for funnel plot asymmetry (Sterne and Egger, 2005).

3. Results

3.1. Overall trends in growth response to monthly metrics

Significant relationships with black spruce tree-ring widths were more commonly found with precipitation than temperature (Fig. 1). Across all sites, 79.5% showed a significant and almost consistently positive relationship between radial growth and precipitation in previous June. By comparison, 42.4% of sites showed a significant relationship with temperature in current July, with direction varying substantially across studies. Black spruce radial growth was generally positively correlated to previous and current summer precipitation, but negatively correlated to precipitation during the dormant season (October to April). Growth was also negatively correlated to current August precipitation. The effect of temperature was less consistent for both previous and current summer, with a higher number of sites showing positive responses compared to negative responses. Significant relationships with dormant season temperatures were scarce (<5% of sites), but generally positive.

Across the spatial range of sites investigated, the proportion of sites showing significant negative and positive responses to monthly climate variables revealed latitudinal trends (Fig. 2). Growth response to previous and current year monthly temperature showed a high amount of variation across latitudes. A high proportion of sites in southern areas (<50°N) showed negative growth responses to mean monthly temperature from previous June to previous August. Towards northern latitudes, such relationships were mostly positive between 50°N and 54°N, and again mostly negative above 54°N. Growth response to mean monthly variables from the previous autumn and winter (September to

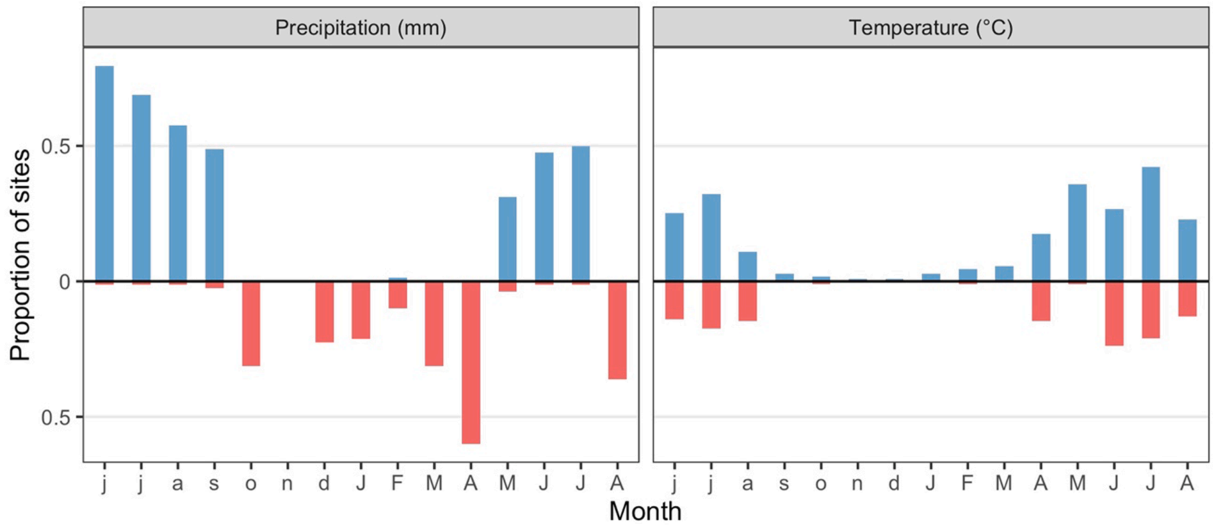

Fig. 1. Response of black spruce to monthly climatic variables based on the results of 11 studies and 113 sampling sites. Bars indicate the proportion of sites showing significant ($\alpha = 0.05$) negative (red) or positive (blue) response to monthly precipitation (left) and mean temperature (right) from previous June to current August. Lowercases and capital letters refer to the month of the previous and current year, respectively. Of the 113 sites, 80 sites investigated the effect of precipitation (78 for previous June) and 109 that of temperature (107 for previous June). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

March) showed no clear spatial trends (Figure S1). In current year spring, particularly in April and May, the proportion of sites characterized by positive growth responses to monthly temperature increased from north to south. For current year June to August, the proportion of sites showing a negative relationship with temperature peaked in the southern areas and decreased towards northern latitudes. For these months, the negative growth response to temperature switched to positive when reaching ~ 50°N, and affected an increasing proportion of sites towards north.

The growth response to previous and current year precipitation showed more consistency compared to temperature. Previous summer precipitation was consistently positive across the latitudinal range investigated. Similarly to temperature, the growth response to previous autumn and winter precipitation showed no clear spatial trends (Figure S1). Sites that showed a negative response to current year April precipitation were restricted to between 48 and 54°N. With the onset of growing season, (May to June), proportions of sites showing positive growth responses decreased with increasing latitude.

3.2. *Influence of site climatic conditions – meta-analysis*

Meta-regressions indicated an influence of site climate and location on correlations between radial growth and monthly temperature (Table 2; Fig. 3), corroborating the patterns suggested by the latitudinal variation in the proportion of sites responding to monthly temperature. Latitude showed the most consistent effect on growth response to temperature, with significant ($p < 0.05$) or marginally significant ($p < 0.1$) effects reported for most of the months investigated (Table 2).

Meta-regressions revealed quadratic relationships between correlation coefficients and latitude for previous summer temperature, which were significant for previous July and marginal for previous August (Table 2; Fig. 3). Similarly, the growth response to previous July temperature showed a quadratic relationship with MAT but that of previous August was non-significant. For previous July, models predicted positive correlation coefficients for sites located between 50°N and 57°N, and with MAT ranging between −5.2 and 0.3 °C, and negative correlations below and above these thresholds.

Marginally significant relationships between previous summer temperature and MAP were also detected, indicating that the correlation with monthly temperature tended to be more positive in wetter areas. Meta-regressions also revealed an influence of site location on the correlation between radial growth and temperature for previous October to February, as correlation coefficients between growth and monthly mean temperature switched to or became more positive as latitude increased and MAT decreased. Conversely, correlation coefficients with March and April temperatures decreased with increasing latitude (Table 2), and switched from positive to negative at ~ 54°N.

In accordance with the latitudinal patterns identified when compiling significant growth responses in Section 3.1, meta-regressions revealed quadratic trends in how MAT and latitude affect the relationships between radial growth and current summer temperature. Models indicated a shift from negative to positive correlations with current year June and July at ~ 51°N and with MAT ranging between −0.6 and 0.5 °C. On the contrary, site climate and location showed little influence on correlation coefficients between growth and monthly precipitation (Table 2). A marginally positive influence of decreasing latitude and increasing MAT was observed for correlations between growth and May precipitation. A marginally negative effect of MAP on correlations between growth and previous December was also recorded.

4. Discussion

Summarizing the results of multiple dendroclimatology studies allowed us to identify key climatic drivers of black spruce radial growth across a large spatial scale in eastern Canada. We found that the direction and consistency of black spruce growth response to both monthly total precipitation and mean temperatures varied seasonally across the 113 sites investigated. Precipitation showed a more frequent influence on black spruce growth than temperature across the study area. The direction of growth-precipitation relationships for a given season was mostly stable and not commonly influenced by latitude, MAT and MAP. Growth-temperature relationships were less consistent and showed strong variation depending on local climatic conditions as revealed through meta-regressions. Overall, climatic conditions during previous and current summer appeared to be the most important determinant of black spruce tree-ring widths. Spring conditions also influenced growth, although to a lesser extent. Dormant season precipitation was negatively related to black spruce growth, whereas temperatures had little influence.

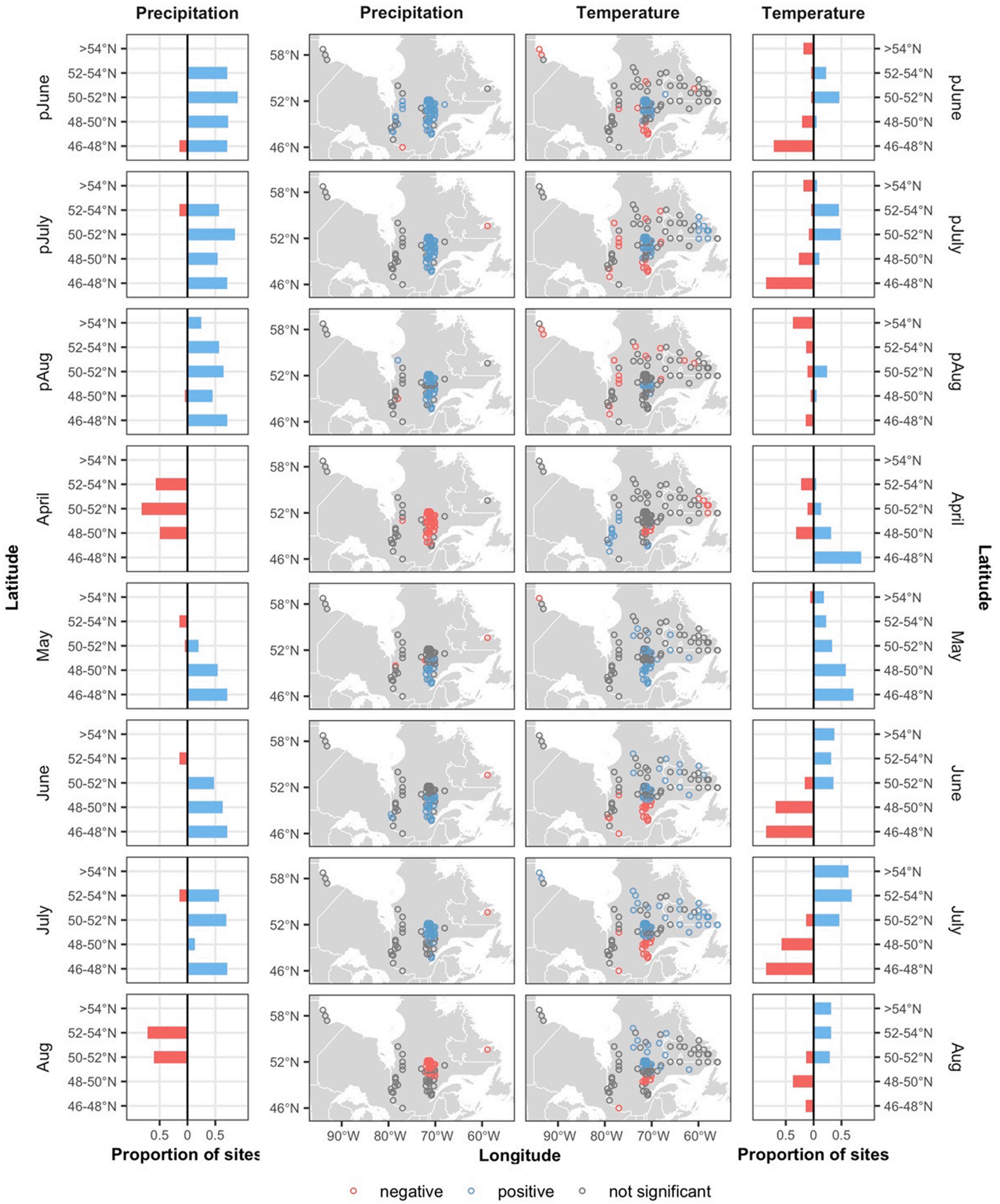

Fig. 2. Growth response of black spruce to monthly climatic conditions based on the results of 11 studies and 113 sampling sites. Each row corresponds to a month, with previous-year months indicated with a p (*i.e.,* pJune refers to previous June). Left and right panels refer to growth response to monthly total precipitation (mm) and mean temperature (°C), respectively. The two outermost columns present the proportion of sites showing significant (α = 0.05) negative and positive responses as a function of latitude. Negative responses are shown in red and positive in blue. Locations indicated by gray symbols on the maps showed non-significant response to the investigated climatic variable. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Influence (estimate ± SE, (p-value)) of site latitude, mean annual temperature (MAT), and mean annual precipitation (MAP) on black spruce growth correlation with monthly temperature (T) and precipitation (P) as evaluated through a meta-regression based on the results of five studies and 24 sites. Only marginal ($p < 0.1$) and significant ($p < 0.05$), results are presented, with significant results in bold. Shaded background indicates a quadratic relationship.

Month	Variable	Latitude (p)	MAT (p)	MAP (p)
pJuly	T	**−0.018 ± 0.006 (0.005)**	**−0.025 ± 0.010 (0.023)**	0.002 ± 0.001 (0.077)
pAugust	T	− 0.008 ± 0.004 (0.051)		0.001 ± 0.0004 (0.058)
pOctober	T	**0.041 ± 0.0064 (<0.0001)**		
pNovember	T	**0.025 ± 0.009 (0.019)**	**−0.028 ± 0.009 (0.001)**	
pDecember	P			−0.001 ± 0.0005 (0.073)
January	T	**−0.006 ± 0.003 (0.045)**		
February	T	0.0096 ± 0.005 (0.080)	**−0.018 ± 0.007 (0.027)**	
March	T	**−0.036 ± 0.013 (0.011)**		
April	T	**−0.033 ± 0.015 (0.036)**		
May	T		−0.012 ± 0.006 (0.080)	
	P	−0.057 ± 0.026 (0.054)	0.045 ± 0.022 (0.075)	
June	T	**−0.008 ± 0.003 (0.027)**	**−0.012 ± 0.006 (0.043)**	
July	T	**−0.015 ± 0.003 (<0.0001)**	**−0.023 ± 0.008 (0.008)**	

4.1. *Summer climate as the main driver of black spruce growth*

Previous summer climate had the most consistent effect on black spruce radial growth. Such findings are similar to results of Marchand et al. (2019) who identified previous growing season climate as the most important driver of black spruce growth in Québec. Black spruce radial growth was correlated with previous and current summer temperature and switched from a negative to a positive response when moving from south to north. This shift in direction of growth response to temperature revealed through meta-analysis supports the hypothesis of a switch from moisture to temperature limitation on growth as suggested by previous studies (D'Orangeville et al., 2016; Sniderhan et al., 2021). During previous summer, excessive heat increases tree transpiration and reduces the accumulation of carbohydrate reserve, leading to a reduced growth in the following spring (Walker et al., 2014; Wolken et al., 2016; Girardin et al., 2016a; Ols et al., 2018; Marchand et al., 2019). Findings from the present meta-analysis support this hypothesis, as increased MAP promoted marginally stronger positive correlations between growth and previous summer temperatures. Cumulative years of excessive heat and drought stress may explain the negative response of growth to current summer temperature (Huang et al., 2010; Drobyshev et al., 2013) observed in the south, as the lagged effect of previous year heat may be greater than the positive effect of current summer temperatures (Girardin et al., 2016a).

Northern latitudes of the boreal forest experience cooler annual temperatures, and consequently lower evaporation stress, compared to southern latitudes. Accordingly, although precipitation is scarcer in northern latitudes, it appears as sufficient to meet the water demand associated with the lower temperatures. Therefore, black spruce trees in northern regions often experience less moisture stress and growth is instead limited by temperature (Nicault et al., 2015; Marchand et al., 2019). This is common in northern boreal trees (Nicault et al., 2015; Trindade et al., 2011; D'Orangeville et al., 2016; Marchand et al., 2019), where warmer temperatures stimulate photosynthesis and therefore carbon assimilation, resulting in a positive effect of warm growing seasons on annual tree growth. Our results support that, in contrast with southern latitude trees, high latitude trees could benefit from the ongoing increase in temperatures (D'Orangeville et al., 2018). This positive effect may however be transitory, as increasing temperatures may eventually exceed an optimum beyond which increased water stress becomes detrimental to growth (D'Orangeville et al., 2018).

For both previous and current summer, a second switch in black spruce growth response to temperature was observed at latitudes above 54 °N with a reduction of correlation coefficients. Temperature usually limits the growth of trees near their northern distribution limit (Thomson et al., 2009; Pedlar and McKenney, 2017; Fréjaville et al., 2020), resulting in stronger positive responses to summer temperature towards northern locations in Québec (Moreau et al., 2020). However, the three northernmost sites that showed negative and weekly positive correlations with previous and current summer temperature, respectively, were also in the most western locations with a distinctive climate characterized by the lowest MAP and MAT of all sites investigated. As a result, the low moisture availability specific of these sites probably limits local black spruce growth and influenced our model predictions. Hence, moisture limitation of black spruce growth may not be restricted to southern latitudes but appears driven by the local temperature to precipitation ratio. This suggest that high latitude stands are not exempt from the negative effect of future warmer temperatures on tree growth, but this requires additional attention for further quantification.

Concerning the generally positive effect of previous summer precipitation on growth, large-scale assessments of black spruce climate-growth relationships reported similar results (D'Orangeville et al 2016; Marchand et al., 2019). This relationship is in accordance with the negative effect of warmer than average previous summers, suggesting a lagged effect of water stress on growth. The relationship with current summer precipitation was mainly positive but restricted to fewer sites.

Although our results suggest a switch from moisture- to temperature-growth limitation towards northern latitudes, we found little influence of local climate on the growth response to monthly precipitation. Such apparent lack of response may be explained by the influence of other site-level factors, such as soil moisture, drainage, and topography (Girardin et al., 2016b; Marchand et al. 2019), which may act at a spatial resolution finer than that of our meta-analysis and prevent us from detecting generalized trends. Indeed, some of the correlation coefficients used as input in the meta-analysis were representative of a group of study sites and did not allow us to investigate variables at such a fine scale. The use of a climate moisture index (CMI) could also help provide a better understanding of the influence of water availability on black spruce growth (Girardin et al., 2016a). Other factors inherent to the methodology used, such as the variability in the timing of the sampling and in the temporal period covered by the input studies, may have also limited our ability to detect trends in growth responses.

4.2. *Influence of spring climate*

A substantial impact of spring climate conditions on black spruce radial growth was observed as indicated by a negative growth response to precipitation and a latitudinal shift in response to temperature, particularly for the month of April. High spring precipitation is likely to be correlated with low solar radiance (D'Orangeville et al., 2016), delaying snow melt and the start of the growing season (Hughes et al., 1999), which can explain the negative growth response to precipitation. This is comparable to winter precipitation, which was consistently associated with negative growth responses across the investigated studies (Figure S1). In addition, negative responses to April precipitation were restricted to locations above 48°N, where it may be comprised of a higher proportion of snowfall, which is likely to further delay the start of the growing season. Negative responses to May precipitation were also observed in the northernmost regions, as correlation coefficients marginally decreased with increasing latitude and decreasing MAT.

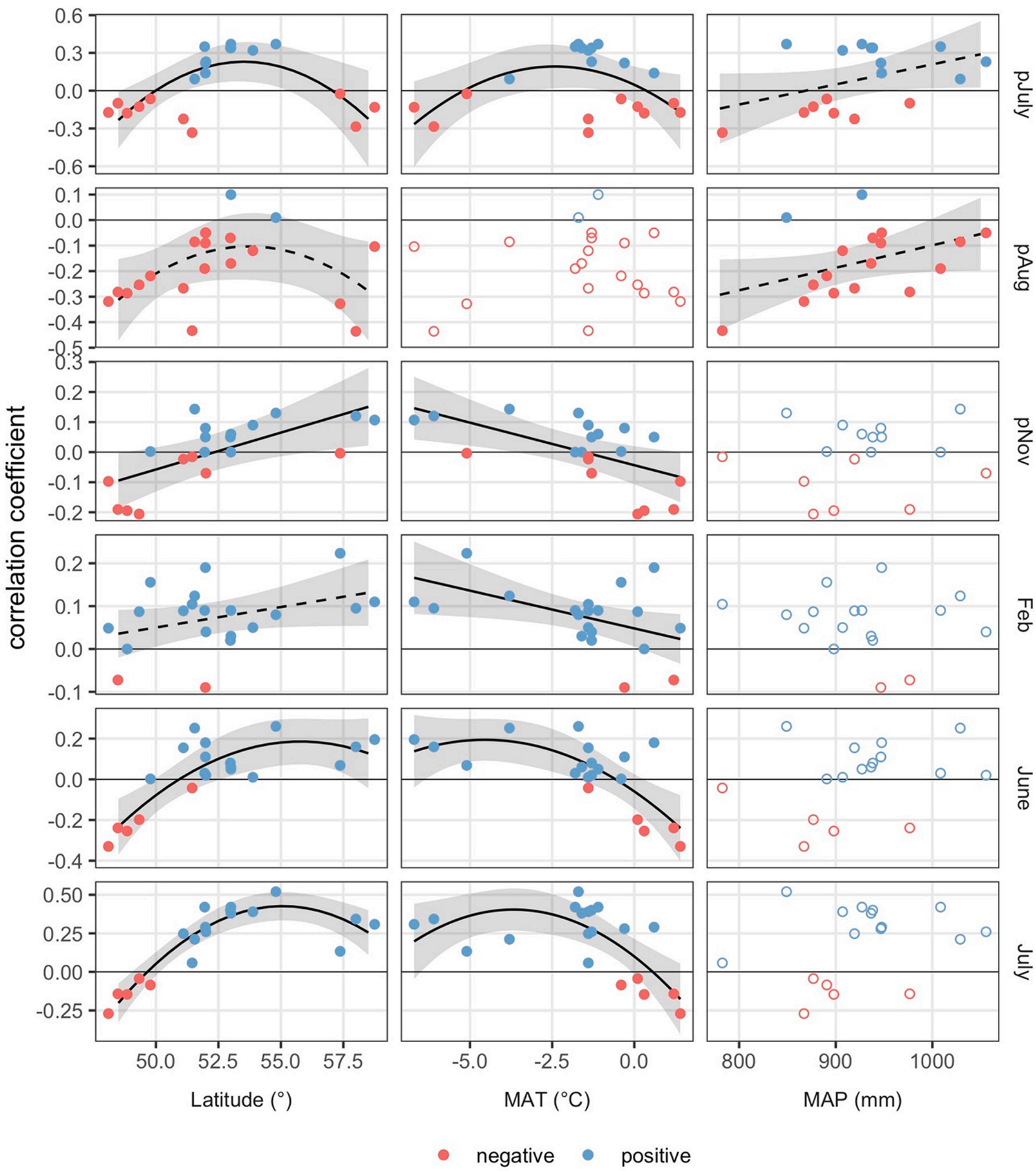

Fig. 3. Effect of site latitude, mean annual temperature (MAT), and mean annual precipitation (MAP) on black spruce growth response to monthly temperature as assessed though meta-regressions based on the results of four studies and 20 sites. Solid and dashed lines represent marginal ($p < 0.1$) and significant ($p < 0.05$) relationships, respectively, with shaded areas representing 95% confidence intervals. Blue and red dots represent positive and negative correlation coefficients reported in the included studies, respectively. Open symbols represent observations for which we found no relationship with site climatic conditions. Only months for which at least two relationships were found are presented. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

These findings coincide with negative growth response in northern sites to April temperatures. The latter may be explained by higher frequency (Marquis et al., 2020) and severity (Moreau et al., 2020) of late spring frosts in northern latitudes, which can induce frost injuries on tree tissues that have de-hardened following a spring thaw. Northern trees may be more vulnerable to late spring frost as a result of their adaptation to shorter growing seasons, which leads them to initiate biological activities at lower temperatures (Aitken and Hannerz, 2001; Kalliokoski et al., 2012). This leads to a greater probability of frost injuries (Suvanto et al., 2016; Chamberlain et al., 2019) and consequently high probabilities of growth declines (Moreau et al., 2020). Below 48°N and with rising temperatures during the month of May, black spruce growth began to consistently respond positively to spring temperatures. Warmer southern spring temperatures are usually associated with an earlier growth onset, leading to a longer growing season, which is known to positively influence black spruce growth (Drobyshev et al., 2010; Girard et al., 2011). This suggests that with future warming, particularly in northern latitudes, black spruce trees are less likely to be at risk from reduced growth due to late spring frosts and may benefit from warmer spring temperatures in May.

4.3. Implications for management

Overall, the results of our study are in line with a transitory beneficial effect of climate warming on tree growth that has been previously reported (Beck et al., 2011; D'Orangeville et al., 2018). This beneficial effect is likely to become limited by water availability, as is already the case in southeastern Canada. Indeed, among the different climate-growth relationships investigated in this study, we observe a shift from negative to positive growth correlations with previous and current summer temperature at mean annual temperatures around 0 °C. Such a threshold is likely to be representative of the limit at which black spruce growth shifts from being moisture- to temperature-limited with increasing latitude. Based on our results, this shift occurred at latitudes between 50 and 51°N. However, this location may have migrated northwards with the warming of the last decades, considering that most of the tree ring series included in the meta-analysis ended at least 10 years ago. By comparison, the MAT threshold we identified in this study is slightly lower than that previously identified in Québec (MAT = 1.1 ± 0.7 °C (SD); D'Orangeville et al., 2016). The difference may be explained by the inclusion of studies conducted west of Québec (Manitoba), where a drier climate is likely to limit black spruce growth at higher latitude. In Québec, it has been suggested that a warming threshold of 2 °C is likely to be the point beyond which boreal forests growth stops being promoted by further warming and starts to decline (D'Orangeville et al., 2018). However, given the heterogeneous landscape across the boreal biome, there is a possibility that many black spruce stands have already reached this point (Marchand et al., 2019).

Whereas such a latitudinal threshold had been suggested in previous studies, our meta-analysis provided a refined understanding of climate-growth relationships by relating them to location-specific climate variables. As a result, our meta-analytic models allow forest managers to easily grasp the variation in growth response to climate at a given location or across a region of interest. Combined with regional climate projections, these models could be used to better anticipate the future growth response. Then, further work will be needed to determine how adaptive silvicultural treatments may induce changes in forest structure or composition to maintain or improve forest productivity over the next century. This is particularly important in southern regions where further warming is likely to promptly increase moisture limitation and could reduce overall boreal forest productivity. Our results could help forest managers prioritize the implementation of adaptive silviculture measures such as stand density management (Jones et al., 2019; Wotherspoon et al., 2020, Moreau et al. 2022) or assisted migration (Isaac-Renton et al., 2014; Napier et al., 2020) in sites experiencing growth reductions associated with drought stress. On the other hand, water limitation could be slowed in some regions as annual precipitation is expected to increase in a majority of sites across Canada (Zhang et al., 2019), though the projected increase in the frequency and severity of drought events (Logan et al., 2011) may prevent such phenomenon. It is therefore imperative that black spruce climate-growth relations continued to be explored across large spatial and temporal ranges so that we can better understand the potential impact of a changing climate on future forest growth as well as its interaction with silvicultural management, soil moisture and other factors.

5. Conclusion

Accounting for black spruce climate-growth relationships in eastern Canada is complex, given the large spatial heterogeneity of the boreal forest. In this study, we compiled as much data as possible to summarize and analyze current research. Monthly precipitation and mean monthly temperature were the most widely used climatic drivers in the literature, though our results suggest that seasonal variables should also be considered in further modelling given the underlying physiological processes leading to consistent growth responses for a given season. The influence of local climatic conditions on the strength and direction of climate-growth relationships also underlines the need to include climate modifiers in the modelling of forest growth. Overall, our results highlight the influence of spring climate on radial growth and the shift from negative to positive response to summer temperature around a MAT threshold of 0 °C between 50 and 51°N. Given projections of future warming and drought events by the end of the century, we are likely to see shifts in forest productivity and species composition in eastern Canada, which will have significant implications for climate mitigation and stand management practices.

CRediT authorship contribution statement

Catherine Chagnon: Conceptualization, Methodology, Writing – original draft, Visualization, Software. **Amy Wotherspoon:** Methodology, Validation, Writing – review & editing. **Alexis Achim:** Supervision, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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